COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, VII
THE XYLEM OF PERESKIAS FROM PERU AND BOLIVIA

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THE PUTATIVE SPECIES OF *Pereskia*, viz. *P. humboldtii* Britt. & Rose, *P. vargasii* H. Johnson, *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd., which occur east of the higher elevations of the Andes in Peru and Bolivia have been described as shrubs or trees varying in height from one to six meters, and having numerous slender terminal branches a few millimeters in diameter. These plants are characterized by the small size of their flowers, fruits and leaves.

The largest stems of which I have succeeded in obtaining anatomical material are six centimeters in diameter in the case of *P. diaz-romeroana*, five centimeters in that of *P. humboldtii*, and three centimeters in that of *P. weberiana*.

The secondary xylem in stems of these representatives of *Pereskia* is of a dense form (FIGS. 1, 2), resembling that which occurs in shoots of comparable diameter in the case of *P. sacharosa* Griseb. described in the preceding paper of this series (Bailey, 1962). As in *P. sacharosa*, the vessels which occur singly and in small clusters are distributed either diffusely (FIG. 2), particularly in the earlier formed secondary xylem, or in more or less zonate patterns (FIG. 1), in subsequently formed wood of large stems. The libriform fibers which commonly are septate and starch containing are abundant and thick walled. The wood parenchyma tends to be scanty paratracheal, but arcs or zones of more abundant parenchyma occur at times, especially where the vessels exhibit zonation in their distributional pattern (FIG. 1). In such arcs of wood parenchyma some cells having very thin unlignified walls occur at times. Furthermore, where multiseriate rays pass through patches of unlignified wood parenchyma their cells also may have unlignified walls as occurs in some stems of *P. aculeata* Mill. (Bailey, 1962). Occasionally in large stems close to the level of the ground, broad zones of unlignified wood parenchyma and ray parenchyma are formed. Such zones may contain isolated clusters of lignified vessels with scanty lignified paratracheal parenchyma.

As in stems of *Pereskia sacharosa*, the multiseriate rays vary in height, breadth and form and in the intervals between them as seen in transverse sections of the xylem (compare FIGS. 1 and 2). When first formed, those which extend outward from parenchymatous gaps in the eustele, tend to

be vertically extensive and subsequently to be dissected into lower deriva-tives (FIG. 3). In the outer xylem of large stems their derivative parts tend to be more or less laterally displaced (FIG. 4), during increasing girth of the cambium. In addition, there is some tendency for the rays to become broader, as well as lower, during their radial extension outward (compare FIGS. 3 and 4). The cells of the innermost part of the first formed multiseriate rays are of "erect" form and subsequently are suc-ceeded by more or less isodiametric and even slightly "procumbent" ones. Such changes in the form and orientation of the ray cells vary in magni-tude and may be precocious or considerably delayed. At times erect cells are retained on the sides and upper and lower margins of the rays (FIG. 4) as in some stems of *P. sacharosa*.

In the third paper of this series (Bailey, 1961b), I noted that where the multiseriate rays of the leaf-bearing cacti are composed throughout of cells with thick, heavily lignified walls deposition of crystals of calcium oxalate when it occurs does so in the form of single crystals or several independent ones, aggregation into druses being absent or of rare oc-currence. On the contrary, where the rays or parts of them are composed of cells with thin, unlignified walls such rays or parts contain numerous druses. Although patches of unlignified ray tissue are of limited and sporadic occurrence in stems of the Andean pereskias, the lignified parts of the rays, as well as the unlignified areas, contain druses. This suggests, as does the occurrence of some druses of rotund form in the outermost layer of the cortex and the character of the foliar vasculature (Bailey, 1960), that in these species there may be tendencies towards trends of phylogenetic modifications such as become exaggerated in *Quiabentia* and *Pereskiopsis*.

In the Peruvian and Bolivian pereskias, as in *Pereskia aculeata*, the primary vascular cylinder and pith vary from one or two millimeters to as much as a centimeter in diameter. Furthermore, as in *P. aculeata*, the number of fascicular strands is fewer than in stems of comparable diameters of *P. sacharosa*. This appears to be correlated with the fact that *P. aculeata* and the Andean pereskias tend to have less modified 2-trace unilacunar nodes than in the case of *P. sacharosa*.

In stems of the Peruvian and Bolivian pereskias, as in stouter young stems of *Pereskia sacharosa*, broadening of the parenchymatous gaps in the eustele allows for an increase in circumference of the primary vascular cylinder and enlargement of the pith after cambial activity is initiated in the fascicular parts. However, there is less broadening of the first formed part of the multiseriate rays than in comparable stems of *P. sacharosa*, two or three rays rather than a single very broad one extending outward from the parenchymatous gaps of the eustele. It should be emphasized in this connection that the tendency for increase in circumference of the eustele and concomitant enlargement of the pith after cambial activity is initiated in the fascicular strands of the primary vascular cylinder becomes increasingly exaggerated and of fundamental significance in more succu-lent forms of cacti.

The underground parts of *Pereskia humboldtii* of Peru and *P. diaz-romeroana* and *P. weberiana* of Bolivia are characterized by having more or less numerous, spindle-shaped and globular, tuberous appearing enlargements which may attain diameters of four centimeters. Some unswollen parts of the underground ramifications fourteen millimeters in diameter, when sectioned and examined with a hand lens, superficially resemble rhizomes in internal structure. As shown in Fig. 6, there is a cylinder of dense secondary xylem enclosing a pith-like core of soft tissue. However, in thin transverse sections (treated with phloroglucin-hydrochloric acid as a test for lignification and examined under higher magnification) one finds that there are no strands of primary xylem subtending the cylinder of lignified secondary xylem, the only remnants of such strands occurring near the center of the axis. Furthermore, the form and radial arrangement of thin-walled unlignified cells in the central core indicate that most of the tissue was formed by cambial activity and contains isolated strands of lignified vessels (Fig. 6).

That such a root structure is due to drastic modification of the derivatives of cambial activity is demonstrated by variations in the internal structure of different roots from the same plant. In some roots, e.g. inner part of Fig. 5, the multiseriate rays are unlignified as in roots of *Pereskia aculeata* (Bailey, 1962). In their extensions outward such rays may exhibit alternations of lignified and unlignified cells. Other roots, while retaining vestiges of a primary body typical of roots, have early cambial activity which forms a larger proportion of unlignified parenchyma. In such roots (Fig. 7) the cambium may subsequently form a cylinder of lignified secondary xylem which at times contains relatively few vessels. This cylinder, as in Fig. 7, may be succeeded in certain cases by an outer zone having a markedly reduced proportion of lignified cells. In larger roots having broad cylinders of normal appearing secondary xylem (Fig. 6) the derivatives of both fusiform and ray initials may have thick lignified walls throughout the cylinder. The vessels which occur singly and in small clusters may be more or less diffusely distributed. In other cases, the vessels exhibit conspicuous zonation in their distribution and patches or arcs of unlignified cells may be present.

Transverse sections cut adjacent to fully matured tuberous enlargements of the roots as shown in Fig. 8 resemble those shown in Fig. 6 in having a cylinder of lignified secondary xylem surrounding a core of unlignified tissue. However, the transition between unlignified and lignified secondary xylem may be less abrupt and uniform, with narrow wedges of lignified tissue extending inward toward the center of the root. Furthermore, the first unlignified cells formed by the cambium exhibit conspicuous enlargement and changes in form and orientation. Particularly between the slender, radially oriented wedges of lignified tissue the enlarged cells have a tangential, rather than a radial, orientation, indicating additional enlargement of the central core of unlignified tissue during early ontogenetic stages of the formation of the root.

The fully matured tuberous swellings of the root system are composed

largely of a greatly enlarged core of unlignified tissue, formed by the cambium and subsequently much expanded by enlargement of its constituent cells. The formation of a tenuous cylinder of lignified secondary xylem is deferred to the final stages of cambial activity (FIGS. 9, 10). In the central core of soft tissue the radial seriation of recently formed derivatives of the cambium becomes displaced and more or less rapidly modified by subsequent enlargement of the unlignified cells (FIGS. 9, 10). Relatively few strands of lignified vessels are formed in the soft tissue. Those that are, become more or less extensively disrupted and displaced during enlargement of the unlignified derivatives of the cambium (FIG. 10). In the few tuberous swellings available to me, the immature ones contain abundant starch, whereas in the case of fully matured ones the central core of unlignified cells contains comparatively little starch. This raises an important question regarding the physiological function of the tuberous enlargements.

In both unswollen and swollen roots examined by me all unlignified parts of the secondary xylem — whether formed by fusiform or ray initials of the cambium — contain some cells with inclusions of druses. However, as in the case of stems, druses also occur in lignified parts of the rays. Furthermore, in all roots there tends to be a precocious and abundant development in the secondary phloem of huge fiber sclereids (FIGS. 7, 9, 10) of a characteristic form discussed in the second paper of this series (Bailey, 1961a).

It is evident that *Pereskia humboldtii* of Peru and *P. diaz-romeroana* and *P. weberiana* of Bolivia are characterized by the potentiality of forming tuberous swellings on their roots. No material of the white-flowered variant of *P. humboldtii*, viz. *P. vargasii*, is available at present. Cárdenas states (personal communication) "the presence of the swellings on the roots of *Pereskia diaz-romeroana* and *P. weberiana*, of variable size (0.5–10 cm.) and either globose or spindle shaped seems to be related to the dry environment in which these plants grow in the wild . . . I have seen in many places those chains of swellings hanging out of the soil where soil was disintegrated by erosion. . . . I have seen *P. sacharosa* in the wild at North Argentina in flat soils with normal roots, that is without swellings. . . . In the low land of Bolivia they used to grow this latter *Pereskia* as fences in flat soils and then too there are no swellings."

These comments of Dr. Cárdenas raise morphological, physiological and taxonomic questions of considerable significance. Is the occurrence of tuberous swellings on the roots of Andean pereskias an "obligate" or "facultative" phenomenon? In other words, do these pereskias form such tuberous enlargements when grown in richer moist soils in level environments? Conversely do other pereskias, e.g. *P. aculeata*, *P. sacharosa*, *P. conzattii* Britt. & Rose, etc., do so when grown in excessively dry habits?

That *P. diaz-romeroana* and *P. humboldtii* form tuberous enlargements in richer moister soils is revealed by plants under cultivation in Norman, Oklahoma, and Berkeley, California. Dr. Boke states (personal communication) "my specimens of *P. diaz-romeroana* (1 year old) have the tuberous

growths of which you speak. They are growing in rather rich soil and they get plenty of water during the summer months." Mr. P. C. Hutchinson writes "I have examined only *P. humboldtii* in the wild, and we have two seedlings of it here, both of which form tubers early in the seedling stages. *P. diaz-romeroana* cultivated outside here from seed, and now mature has formed them also on all plants." Therefore, it appears probable that the formation of tuberous enlargements is a genetically "obligate," rather than a "facultative," phenomenon in the case of *P. humboldtii* and allied taxa. Thus it appears to be a significant diagnostic characteristic of these pereskias.

My material of roots of other pereskias does not have tuberous enlargements. The swollen roots of pot-bound plants are not homologous anatomical structures. Mr. Hutchinson states (personal communication) "As to whether other species than these three form such structures, so far as we know, they do not." Therefore, whether other pereskias ever form tuberous enlargements when growing under unusual environmental influences must remain for the present an inconclusively answered question.

DISCUSSION

Although the secondary xylem in stems of the Andean pereskias in general resembles that in shoots of comparable sizes of *Pereskia sacharosa*, it differs in the sporadic occurrence of small patches of unlignified tissue and in the common occurrence of druses of calcium oxalate in its lignified multiseriate rays. It is in their roots that the Andean pereskias differ most drastically from *P. sacharosa* and exhibit possible relationships to *P. aculeata*.

Many roots of *Pereskia sacharosa* are of normal dicotyledonous structure, the multiseriate rays throughout their radial extension being composed of cells having relatively thick, lignified secondary walls. However, in some roots of this species the inner parts of the first-formed multiseriate rays close to the primary xylem are unlignified. Such unlignified parts do not contain druses of calcium oxalate and little if any starch, their cells being packed with granular contents of at least semi-proteinaceous composition.

This tendency for the elimination of secondary walls and lignification in derivatives of the cambium, although detectable at times in stems of the Andean pereskias, obviously becomes much exaggerated in their root system, culminating in the formation of tuberous enlargements. The unlignified tissue of these plants, as that formed in both stems and roots of *Pereskia aculeata*, differs from *P. sacharosa* in containing numerous druses of calcium oxalate and more or less abundant starch. One may suspect from a physiological point of view that the much exaggerated tendency toward the formation of druses of calcium oxalate in roots of the Andean pereskias is extended into the lignified rays of the stem.

As demonstrated in the second paper of this series (Bailey 1961a), there are three distinct categories of pereskias which can be differentiated by consistent differences in the form and distribution of sclereids in their second-

ary phloem. *Pereskia aculeata*, the Andean pereskias, and species from southern Mexico and Central America occur in one of these categories, whereas *P. sacharosa* together with *P. grandifolia, P. bleo, P. corrugata* and *P. tampicana* occur in a second category.

In the preceding paper of this series (Bailey, 1962), it was shown that the vinelike habit of growth and the secondary xylem of *Pereskia aculeata*, in contrast to those of *P. sacharosa*, tend to negate any possibility of considering this species to be one of the most, if not the most, primitive living representative of the Cactaceae. Similarly the highly modified structure in roots of the Andean pereskias negates the conclusion that these species have retained primitive structures in all of their organs and parts. Indeed, available evidence indicates that in the Cactaceae, as in many other families of angiosperms, trends of phylogenetic specialization in reproductive and vegetative parts are not always closely synchronized. Reliable clues regarding the form and internal structure of ancestral Cactaceae, in the absence of fossils in the geological record, can be obtained at present only by synthesizing evidence from all organs and parts of surviving genera and species. Of pereskias thus far dealt with in this series of papers, *P. sacharosa* is significant in having less advanced specializations in both its flowers and its secondary xylem. Therefore, it will be of interest from both phylogenetic and taxonomic points of view to compare the form and internal structure of this species with those of pereskias from southern Mexico and Central America, from eastern and northern South America and from the West Indies.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. Transverse and tangential longitudinal sections of the secondary xylem of stems. 1, Transverse section of the outer secondary xylem of a large stem of *Pereskia diaz-romeroana* [*Cárdenas*], × 11. 2, Transverse section of the inner secondary xylem of *P.* aff. *humboldtii* [*Ferreyra 14200*], × 11. 3, Tangential section of the outer secondary xylem of *P. weberiana* [*Cárdenas*], × 43. 4, Tangential section of the outer secondary xylem of larger stem of *P. diaz-romeroana* [*Cárdenas*], × 43.
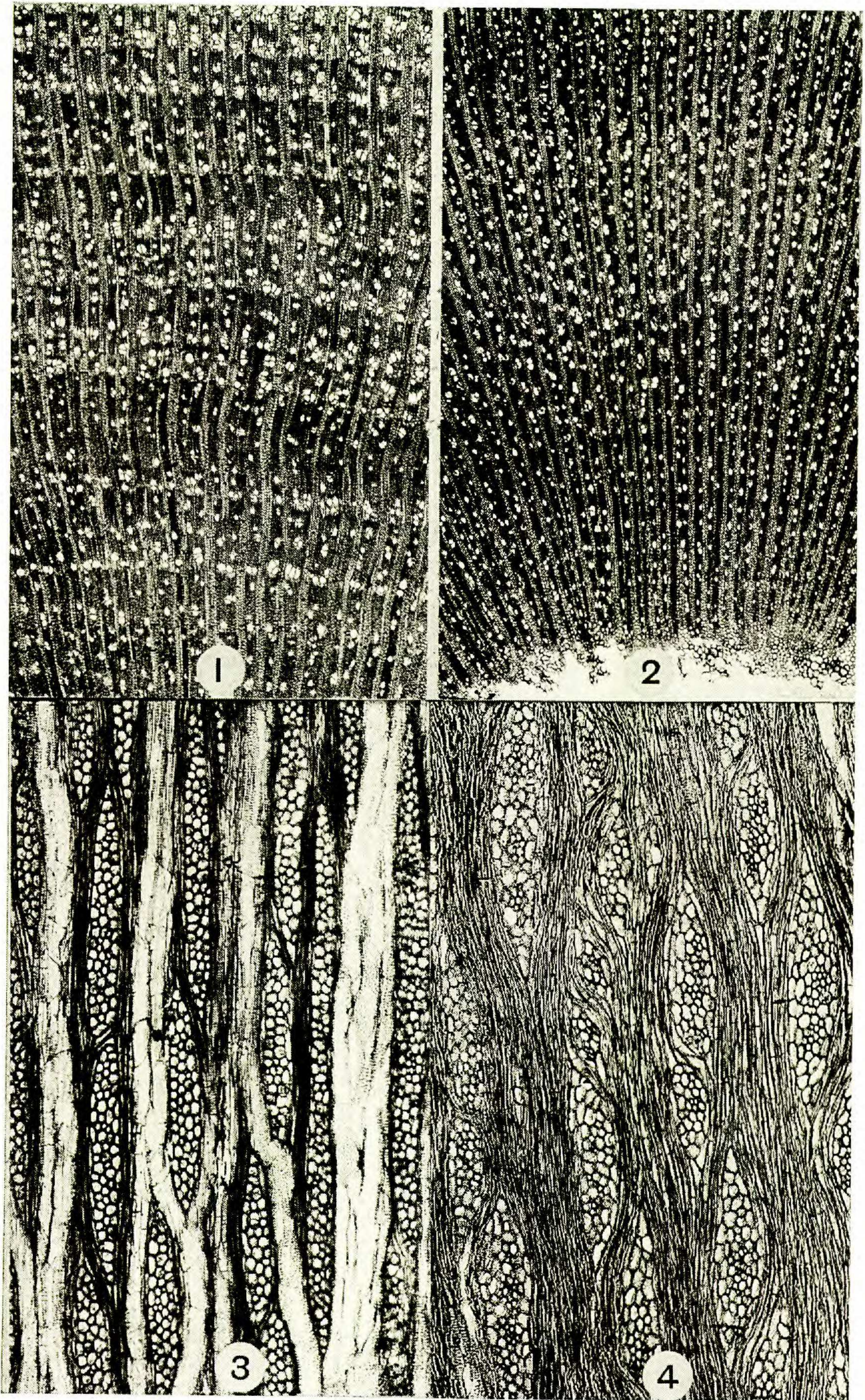
PLATE II

FIGS. 5–6. Transverse sections of roots treated with phloroglucin-hydrochloric acid. 5, Xylem of *Pereskia weberiana* [*Cárdenas*] showing unlignified parts (white) of multiseriate rays, × 34. 6, Xylem of *P.* aff. *humboldtii* [*Ferreyra 14204*] showing central core of unlignified tissue (white) which contains scattered strands of lignified vessels and abundant druses of calcium oxalate in its central part, × 11.

PLATE III

FIGS. 7–8. Transverse sections of roots treated with phloroglucin-hydrochloric acid. 7, Slender root of *P.* aff. *humboldtii* [*Ferreyra 14204*] showing unlignified parts of xylem (white), also the occurrence of fiber-sclereids in the outer secondary phloem and cortex, × 22. 8, Section of root adjacent to spindle-shaped tuberous swelling of *P.* aff. *humboldtii* [*Ferreyra 14204*], × 11.
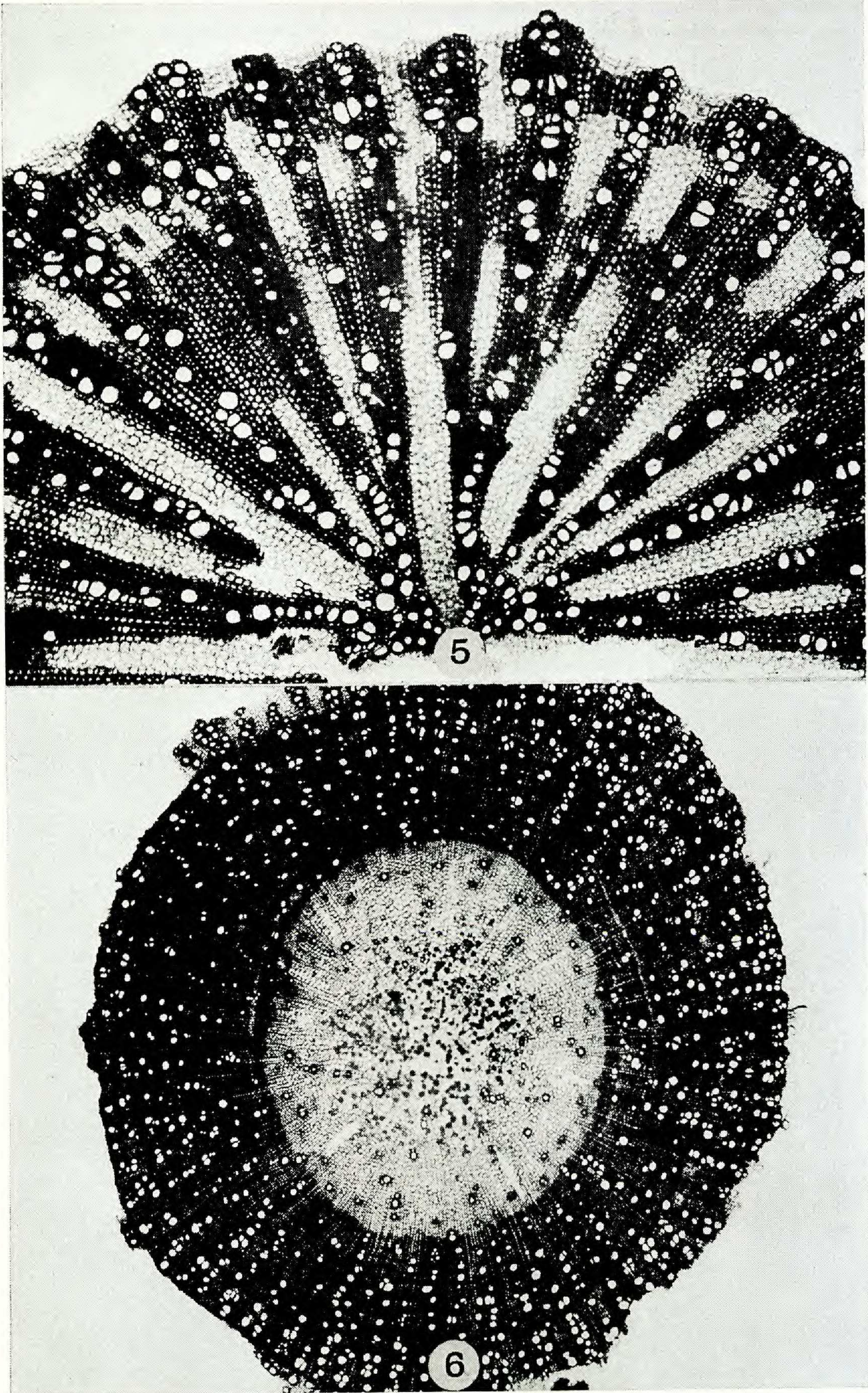
PLATE IV

FIGS. 9–10. Transverse and radial longitudinal sections of fully matured tuberous enlargement of *P.* aff. *humboldtii* [*Ferreyra 14204*], treated with phloroglucin-hydrochloric acid, × 11. 9, Transverse section showing part of the huge core of unlignified tissue (light), narrow outer zone of lignified secondary xylem (dark), abundant fiber-sclereids in the outer secondary phloem, and the occurrence of druses in many cells of the unlignified core. 10, Radial section showing the same structural features, also disruption of isolated strands of lignified vessels during enlargement of derivatives of the cambium in the central part of the unlignified core. In this section most of the druses were dissolved during prolonged treatment in phloroglucin-hydrochloric acid.
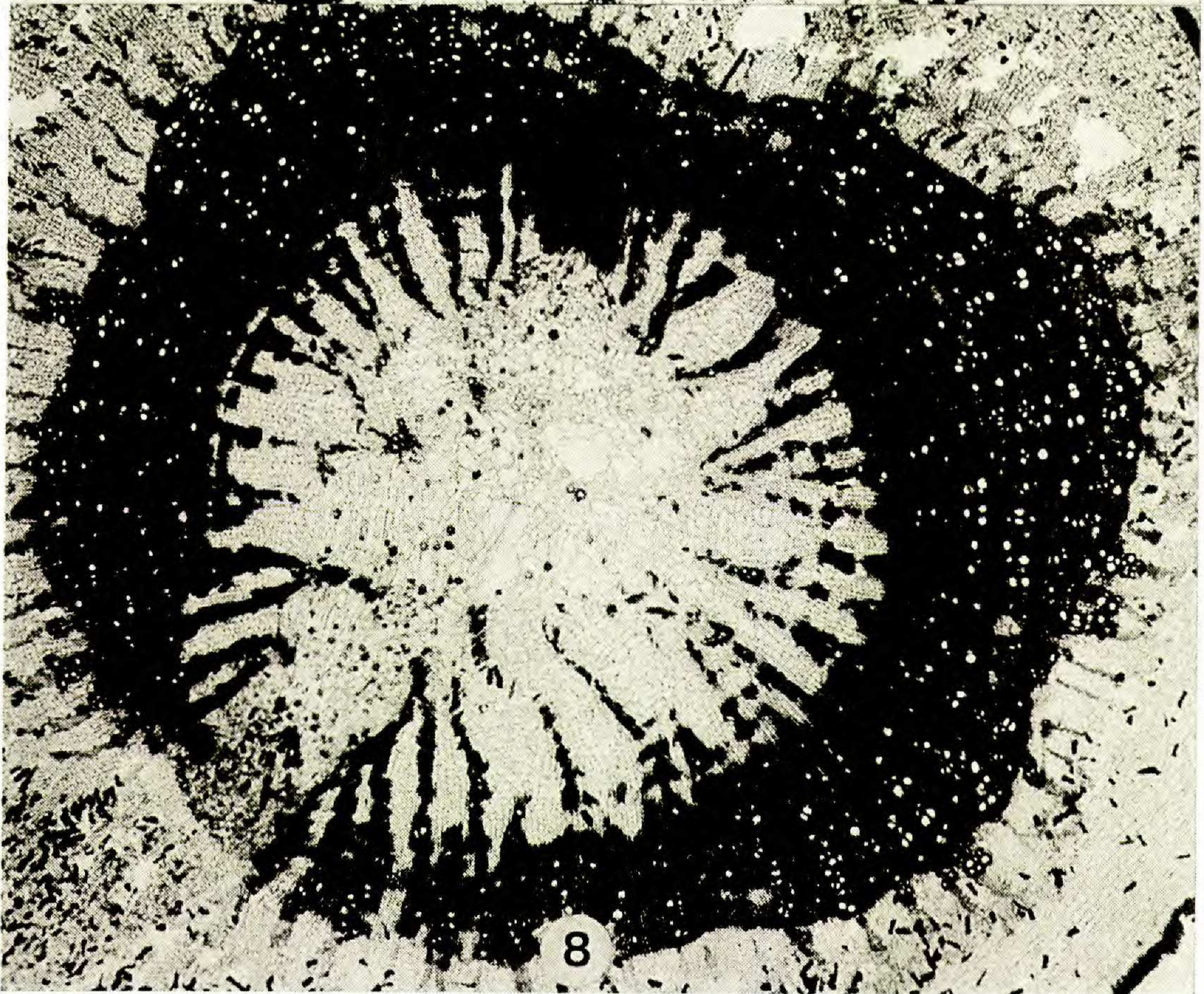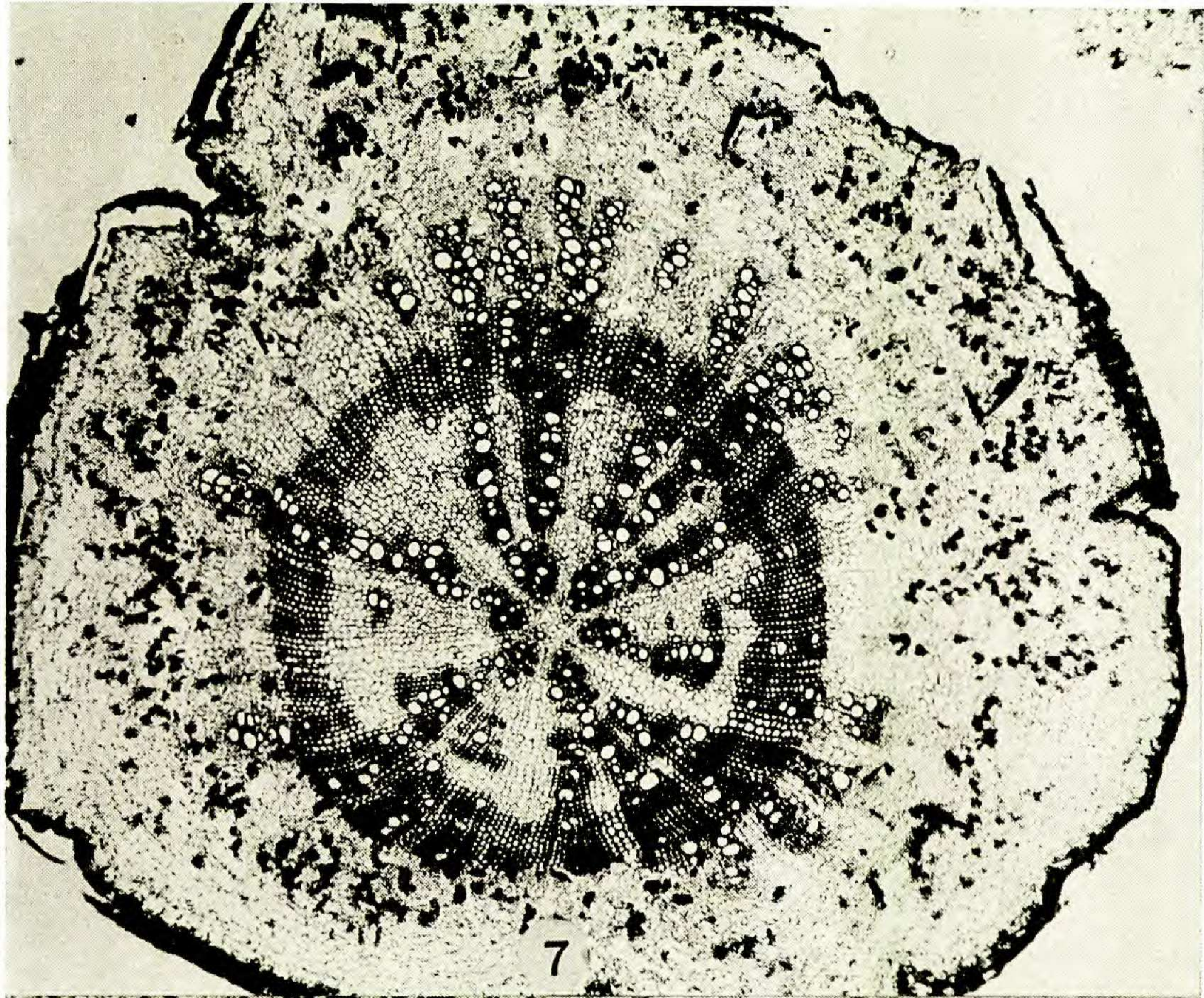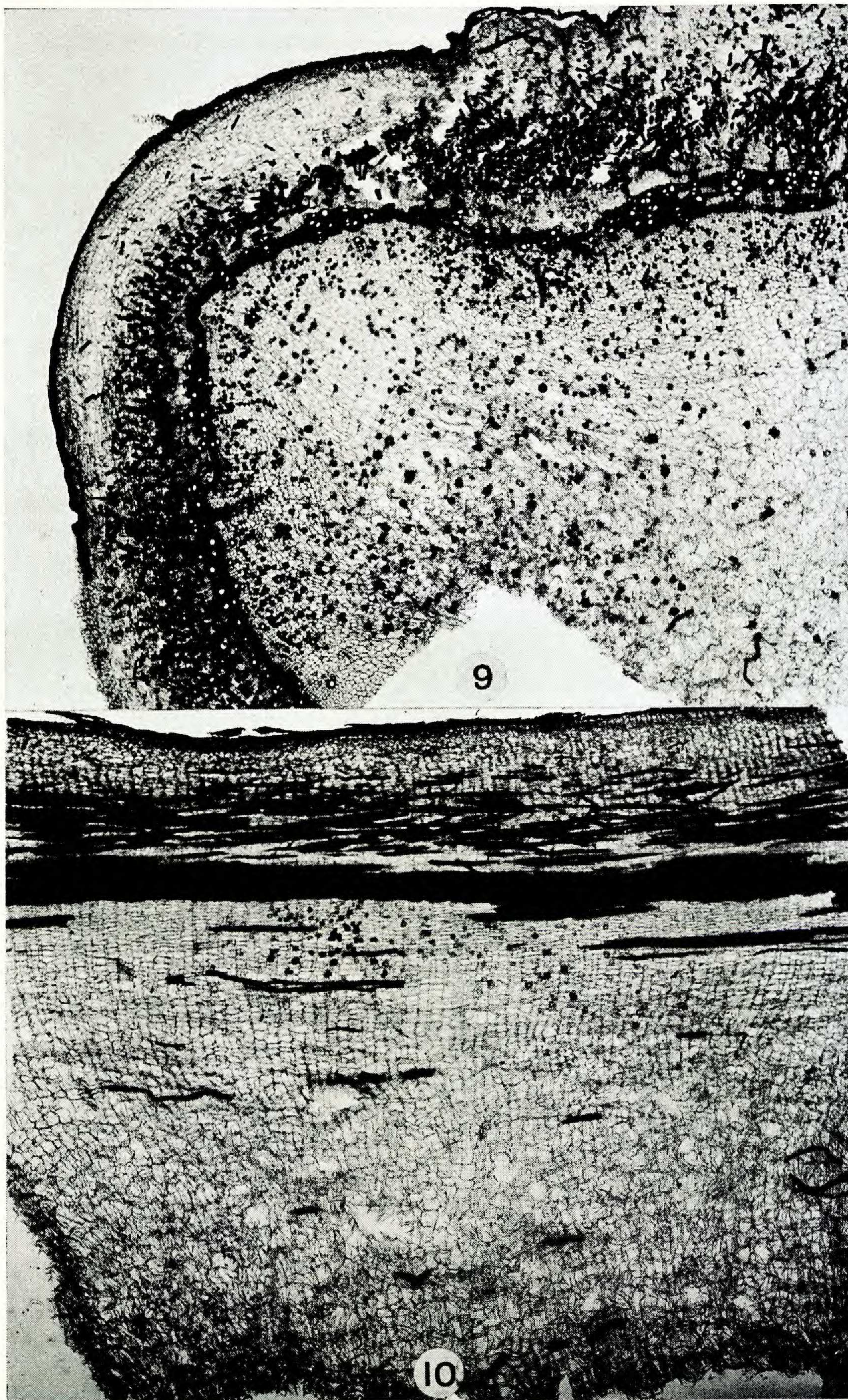
Plate I

Plate II

Bailey, Leaf-bearing Cactaceae, VII

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BAILEY, LEAF-BEARING CACTACEAE, VII